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Feeding selectivity and rapid particle processing by deep-sea megafaunal deposit feeders: A ^{234}Th tracer approach

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ABSTRACT

Deposit-feeding megafauna occur in virtually all deep-sea environments, yet their feeding selectivity and particle processing rates are poorly known. Excess ^{234}Th activity is commonly used as a geochemical tracer for recently settled (<100-d old) particles in the quiescent deep sea, but it has rarely been applied to the study of deposit feeders. To explore the selectivity and rates of megafaunal deposit feeding, we compared excess ^{234}Th activities in the gut contents of deposit feeders from Santa Catalina Basin (SCB) (~1200 m depth) and the Hawaiian slope (~1680 m) to the activity of surface sediments and, in SCB, to material from sediment traps moored ~150 m above the seafloor. We also measured concentrations of chlorophyll *a* and phaeopigments in animal guts and surface sediments to evaluate feeding selectivity. In the SCB, excess ^{234}Th ($^{234}Th_{xs}$) activities in the guts of four species of surface-deposit feeders were 14–17 fold greater than those of the top 5 mm of sediment. *Pannychia moseleyi* and *Scotoplanes globosa,* two highly mobile, surface-deposit-feeding elasipodid holothurians, were the most enriched in gut $^{234}Th_{xs}$ activity, suggesting that these species fed very selectively on particles settled to the seafloor within the previous ~20 d. *Pannychia moseleyi* guts also exhibited 500-fold enrichment of chlorophyll *a* relative to surface sediments indicating highly selective ingestion of phytodetritus. *Chiridota* sp., a burrowing, surface-deposit-feeding, chiridotid holothurian, and *Bathybembix bairdii,* a surface-deposit-feeding trochid gastropod, were less enriched in gut $^{234}Th_{xs}$ activity, reflecting lower mobility and/or less selectivity at time of particle pickup. A subsurface-deposit-feeding, molpadiid holothurian was not enriched in gut $^{234}Th_{xs}$ activity compared to surface sediments, but was greatly enriched compared to average activities at its presumed feeding depth of 6–7 cm. On the Hawaiian slope, gut contents of two surface-deposit feeders, the synallactid holothurians *Mesothuria carnosa* and *Paleopatides retifer,* were not enriched in $^{234}Th_{xs}$ activity; however, *M. carnosa* and *Phryssocystis* sp. (a surface-deposit-feeding echinoid) were enriched in chlorophyll *a*, suggesting that the Hawaiian slope species are also selective feeders. Presumably, frequent sediment resuspension makes $^{234}Th_{xs}$ activity a poor tracer for recently settled, food-rich particles on the Hawaiian slope. Based on a newly developed ^{234}Th-flux model, we calculate that the three dominant megafaunal, surface-deposit feeders in SCB consumed on average 39–52% (s.e. 13–27%) of the daily flux of $^{234}Th_{xs}$ activity to the SCB floor. By chemically altering (e.g., digesting) and redistributing recently settled particulate organic matter, these megafauna are likely to substantially influence carbon diagenesis and food-web structure in this bathyal habitat.

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1. Introduction

Deposit-feeding megafauna occur in virtually all bathyal and abyssal habitats (e.g., Gage and Tyler, 1991). Because these large, relatively sparse animals are rarely collected in quantitative seafloor samples, their effects on community-level processes and sediment geochemistry are easily overlooked. However, time-lapse photographic studies at a number of sites on the continental margin suggest that megafauna may traverse substantial portions of the seafloor over time scales of days to months (e.g., Lafond, 1967; C. Smith, 1992; K. Smith *et al.,* 1993). If these animals selectively ingest recently settled particles, they could process a substantial proportion of the labile particulate-organic-carbon (POC) flux reaching the bathyal seafloor. Such ingestion will physically alter settled particles through gut compaction and fecal-pellet formation (e.g., Taghon *et al.,* 1984), it will change the chemical composition and microflora of fresh particles through digestion and redox alterations (e.g., Plante and Jumars, 1992), and it will concentrate labile POC into fecal deposits and burrow lumens (e.g., Jumars and Wheatcroft, 1989; C. Smith *et al.,* 1986, 1996). In addition, such selective ingestion may lead to age-dependent mixing, wherein recently settled, food-rich particles are mixed faster into the sediment column than are older, food-poor particles (C. Smith *et al.,* 1993). All of these processes will affect the quality and availability of labile POC to other members of the bathyal benthos and will modify the nature and distribution of organic-carbon diagenesis in deep-sea sediments.

The particle selectivity of deep-sea deposit feeders is relatively poorly known, although it is expected to be high. Shallow-water deposit feeders of many taxa, especially those feeding near the sediment-water interface, select particles based on small size, low specific gravity and presence of organic coatings (see reviews in Wheatcroft (1992) and C. Smith *et al.* (1993)). Because the deep sea is a relatively organic-poor environment, with labile POC primarily sinking from overlying waters, deep-sea deposit feeders are likely to preferentially consume recently settled particles using mechanisms similar to their shallow-water counterparts (C. Smith *et al.,* 1993). In fact, a variety of megafaunal deposit feeders from the abyss are known to selectively ingest or sequester chlorophyll-*a*-rich, phytodetrital material that is newly arrived at the seafloor (Billet *et al.,* 1988; Thiel *et al.,* 1989; Moore and Roberts, 1994; Roberts *et al.,* 1996; C. Smith *et al.,* 1996). Diatom-addition experiments using ^{13}C-labeled algae also imply rapid uptake of fresh phytodetritus by a variety of macrofaunal surface-deposit feeders from bathyal depths (Levin *et al.,* 1997).

In this study we use excess ^{234}Th ($^{234}Th_{xs}$) activity as a natural tracer to explore particle selectivity and particle processing rates of bathyal deposit feeders. $^{234}Th_{xs}$ is scavenged by particles settling through the water column and has a radioactive half life of 24.1 d; it thus may be used to trace the behavior of particles for roughly 100 d after they have reached the seafloor (e.g., Aller and DeMaster, 1984; C. Smith *et al.,* 1993). In earlier work, we predicted that in quiescent deep-sea habitats, deposit-feeder gut sediments should be substantially enriched in excess ^{234}Th activity due to selective feeding on recently settled, food-rich particles (C. Smith *et al.,* 1993). A recent study (Lauerman *et al.,* 1997) has, in

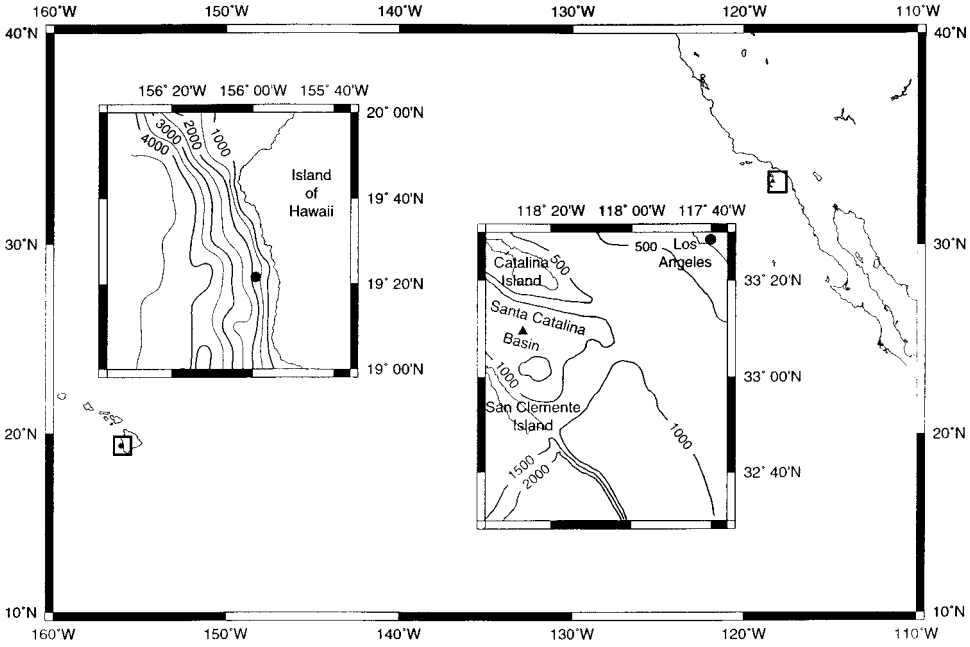

Figure 1. Locations of study areas on the Hawaiian slope (circle) and in Santa Catalina Basin (triangle). Contours are in meters.

fact, found high excess ^{234}Th activities in the gut sediments of two abyssal species of holothurians on the California margin.

Here we further test our predictions of feeding selectivity in megafaunal deposit feeders using $^{234}Th_{xs}$ and chlorophyll-*a* measurements in the quiescent Santa Catalina Basin, and on the physically more energetic Hawaiian slope. In particular, we compare the feeding selectivity of eight species of deposit feeders from three classes (holothurians, echinoids and gastropods) belonging to the three different feeding guilds (highly mobile, epibenthic surface-deposit-feeders; borrowing surface-deposit feeders; head-down subsurface-deposit feeders). In Santa Catalina Basin, we also develop a new tracer approach, using excess ^{234}Th activity, to evaluate the processing rates of recently settled particles by megafaunal populations. We find that the often overlooked deposit-feeding megafauna can feed very selectively on recently settled (or "young") particles and could substantially influence the diagenesis and availability of labile POC in at least some bathyal and abyssal habitats.

2. Study sites

Santa Catalina Basin (SCB) is a flat-bottomed basin of about 1220 m depth (Fig. 1); our study area was a square roughly 8 km on a side centered at 33° 9.5′ N, 118° 28′ W. Actual stations ranged in depth from 1212 to 1240 m (station details are available upon request from C. Smith). Bottom sediments in SCB are poorly sorted clayey silt, with sedimentation

rates of 12–21 cm per 1000 years (Emery, 1960; DeMaster *et al.,* in prep.). Bottom-water oxygen concentrations are 18–23 micromolar (Archer *et al.,* 1989), the physical environment is relatively low-energy (we have never observed currents of erosive magnitudes in over 50 submersible dives and 3 months of time-lapse camera deployments), and the fauna is well described (C. Smith, 1985, 1986). Deep POC flux in the general area appears to be relatively constant throughout the year [e.g., ranging from 0.02–0.06 g/m^2/day in the nearby San Pedro Basin (Thunnel *et al.,* 1994)].

The Hawaiian slope site (19° 36′ N, 156° 4′ W) is west of the island of Hawaii, on a ~1680-m deep platform at the base of a 22° slope (Fig. 1). During two submersible dives, we saw no evidence of sediment transport, although sediments were difficult to penetrate with cores. Our sampling area ranged in depth from 1680 to 1685 m and was sediment-covered, with occasional rock outcrops. Hawaiian waters are characterized by relatively low productivity and seasonality (e.g., Karl and Lukas, 1996). The deep-sea megafauna of this region is described in Chave and Jones (1991).

3. Methods

a. Field methods

In SCB, we collected five common species of deposit-feeding megafauna in Dec 1995 and Jan 1996: the epibenthic surface-deposit feeders *Pannychia moseleyi, Scotoplanes globosa* (elasipodid holothurians), and *Bathybembix bairdii* (trochid gastropod); the burrowing, surface-deposit-feeding holothurian *Chiridota* sp.; and the head-down (conveyor-belt) deposit-feeder *Molpadia* sp. (molpadiid holothurian). On the Hawaiian Slope in Oct 1996, we studied the epifaunal surface-deposit feeders *Mesothuria carnosa* (synallactid holothurian), *Paleopatides retifer* (synallactid holothurian), and *Phryssocystis* sp. (echinoid). Epibenthic megafauna were collected in SCB with the submersible *Alvin* (dive nos. 3048–3054) and on the Hawaiian slope using the Hawaiian Undersea Research Laboratory submersible *Pisces V* (dive nos. 317–318) with a scoop net. Megafauna in SCB (in particular *Molpadia* sp., *Scotoplanes,* and *Chiridota* sp.) were also collected with a 8-m semi-balloon otter trawl (outer mesh 3.8 cm, inner mesh 1.3 cm) deployed from the RV *New Horizon* or RV *Atlantis II. Chiridota* sp. were also recovered from several USNEL-type, 0.25 m^2 box-core samples. Animals were dissected within two hours of recovery and the gut contents frozen. Material used for pigment analysis was frozen in liquid nitrogen and stored at −80°C. Holothurian foreguts were identified by the restricted area separating them from the "hindgut" [i.e., the intestine, rectum and cloaca (Roberts *et al.,* 1996)]. Depending on the size of the individual gut, hindgut contents were frozen whole or divided into 2–4 sections. Owing to small animal size, we combined gut sediments of *Chiridota* sp. (10 individuals per group) and *Bathybembix bairdii* (3–5 per group) to provide adequate mass for radiochemical analyses.

In SCB, sediment cores were collected with *Alvin* using an Ekman box corer (20 × 20 cm, with 4 10 × 10-cm subcores) or *Alvin* tube corer (6.8-cm diameter). In addition, 10-cm diameter cores were taken in SCB using a multiple corer (Gage and Tyler, 1991). Tube

cores (6.8-cm diameter) were taken on the Hawaiian Slope with the *Pisces V.* Cores were extruded and sectioned into depth intervals as in C. Smith *et al.* (1993), cutting away about 5 mm of the periphery of each depth interval to avoid contamination from vertical smearing. In SCB, cores were sectioned at 0.5-cm intervals to a depth of 2.0 cm, and at 1-cm intervals below 2 cm. On the Hawaiian slope, cores were sectioned into 0–0.2 and 0.2–0.5 cm depth intervals, and then at 0.5 cm intervals to the core bottom. Depth intervals were homogenized, split for analyses and frozen. Pigment samples were frozen in liquid nitrogen and stored at −80°C.

Replicate, single-cup sediment traps of the type used by Dunbar *et al.* (1989) were deployed 150 and 170 m above bottom in SCB for 32.8 days beginning on 5 December 1995. Trap samples were preserved *in situ* using a hypersaline formalin solution (5% NaCl w/w, 10% formalin by volume), and swimmers were removed from samples after recovery.

To evaluate the abundance of epibenthic megafauna in SCB, photographic transects were conducted using *Alvin*'s sponson camera as in Smith and Hamilton (1983), with *Alvin* skiing along the bottom to maintain constant height, traveling at ∼15 m/min on a random heading, with an exposure interval of 15 s. The three phototransects were an average of 537 ± 56 (s.e.) m long with a mean of 143 ± 15 photographic frames each.

b. Laboratory methods

$^{234}Th_{xs}$ activity was measured using a variation of the technique of Aller and DeMaster (1984), as described in Pope (1992). Briefly, ^{234}Th activity was isolated and then measured on a low level, gas flow, anti-coincidence beta counter. ^{238}U activities were measured by alpha spectroscopy. ^{234}Th activities were converted to excess values by subtracting ^{238}U activity from total ^{234}Th activity and correcting for decay since sample collection. All excess ^{234}Th activities are expressed in dpm g^{-1} dry sediment (corrected for salt content).

For pigment analyses, samples of frozen gut and core sediments (∼2 g) were vortexed, sonicated in a dark ice bath for 10 minutes, and extracted overnight at −20°C in the dark in 10 ml of 100% acetone in glass tubes (Stephens *et al.,* 1997). Acetone extraction may reduce degradation artifacts associated with fluorometric measurement of chlorophyll-*a* (Jeffrey and Hallegraeff, 1987). Samples were then centrifuged for 5 min and the absorption of the supernatant at 670 nm read on a Turner model 10-AU fluorometer. Phaeopigments were measured using the acidification technique (Strickland and Parsons, 1972). Chlorophyll *a* (chl-*a*) and phaeopigment concentrations were calculated based on a standard solution from Fisher Scientific. Values were normalized to salt-corrected dry weights of extracted sediment. Sun *et al.* (1991) reported 90.6 ± 3.1% recovery of standard chl-*a* from wet sediments using fluorometry; we judged this level of accuracy acceptable for measuring concentrations of chl-*a* as an indicator of the presence of fresh phytodetritus.

Gut enrichment factors (EF) for $^{234}Th_{xs}$ activity and chl-*a* concentrations were calculated as the ratio of gut activity or concentration to surface-sediment activity or concentration. Average gut enrichment factors were calculated for each sampling period (Dec 1995 and Jan 1996) using surface sediment collected at the same time (Table 1). Overall means were

Table 1. $^{234}Th_{xs}$ activities, chlorophyll *a* concentrations, mean enrichment factors (EF) and apparent $^{234}Th_{xs}$ ages of SCB surface and gut sediments compared to corrected sediment-trap activity. Chlorophyll *a* gut concentrations are for foreguts; enrichment factors for them are as compared to surface sediment. SCB is Santa Catalina Basin, and HS is Hawaiian Slope. Data are means ± one standard error.

Sample	Date	$^{234}Th_{xs}$ (dpm/g)	EF	*n*	Chl *a* (μg/g)	EF	*n*	Apparent $^{234}Th_{xs}$ age (d)
SANTA CATALINA BASIN:								
Sediment trap (uncorrected)	12/5/95–1/7/96	1260 ± 95		2				
Sediment trap (corrected)	12/5/95-1/7/96	1960 ± 150		2				0
Surface sediment (0–5 mm)	12/95	30.9 ± 2.4		3				143
Surface sediment (0–5 mm)	1/96	4.9 ± 0.9		3	0.36 ± 0.09		2	207
Subsurface sediment (6–7 cm)	12/95	0 ± 0		3				
Subsurface sediment (6–7 cm)	1/96	0 ± 0		6				
Pannychia moseleyi	12/95	2730 ± 300	88 ± 11	3				−11.4
Pannychia moseleyi	1/96	1290 ± 90	261 ± 57	6	200.77 ± 71.90	558 ± 399	4	14.4
Chiridota sp.	12/95	767 ± 50	25 ± 6	3				32.4
Chiridota sp.	1/96	114 ± 7	23 ± 1	3				98.1
Bathybembix bairdii	12/95	883 ± 90	29 ± 13	3				27.5
Bathybembix bairdii	1/96	144 ± 14	29 ± 6	2				90.0
Scotoplanes globosa	12/95	2290 ± 195	74	1				−5.4
Molpadiid holothurian	12/95	4.1 ± 0.5	0	3				212.7*
HAWAIIAN SLOPE:								
Surface sediment (0–2 mm)	10/96	2.0 ± 0.9		1	0.44 ± 0.01		3	
Phryssocystis sp.	10/96				5.15 ± 0.43	12 ± 4	3	
Mesothuria carnosa	10/96	3.2 ± 0.5	2 ± 1	2	1.18 ± 0.34	3 ± 2	2	
Paleopatides retifer	10/96	2.9 ± 1.1	1 ± 1	3				

*Age compared to surface sediment is 51 d.

calculated as the average of the means from the two sampling period (Dec 95 and Jan 96, yielding $n = 2$) (Fig. 2), again compared with the mean of sediment from the same time period.

Population densities of *Pannychia moseleyi, Chiridota* sp., and *Bathybembix bairdii* in SCB were estimated from *Alvin* photographic transects. Each photographic frame was projected onto a perspective grid (McNeil, 1954), provided by the *Alvin* Group, using a Besseler model 23CII enlarger. Animals were counted from a 2.25 m^2 square in the central foreground of each frame where they were clearly identifiable. Mean organism density for each transect was calculated as an independent estimate of abundance for the study area. The three transect means were then averaged to yield an overall mean and variance.

Because *Chiridota* sp. could not be resolved in transect photos due to its small size and burrowing habits, its densities were estimated from seven sets of vertical, close-up, time-lapse photographs taken at 0.8–8 hr intervals from a free-vehicle camera system (the "moundster" camera) deployed at our SCB site in 12/86 ($n = 3$), 1/87 ($n = 2$) and 10/87

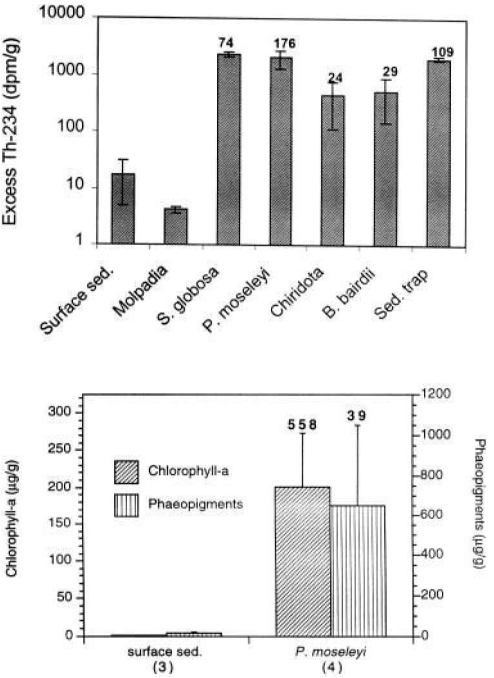

Figure 2. Top: Mean $^{234}Th_{xs}$ activities in the surface sediment (0–5 mm), deposit-feeder guts, and sediment-trap material from Santa Catalina Basin. Note that $^{234}Th_{xs}$ activity is plotted on a log scale. Where possible, means given are the average of the two means for the Dec and Jan sampling times; *Scotoplanes, Molpadia* and sediment-trap samples were collected only at one time so the mean of all individuals collected is given. Error bars = one standard error, with the exception of *Scotoplanes globosa* ($n = 1$), where the error is a 1 σ counting error (see text). Numbers above the histograms are mean enrichment factors relative to surface sediment. Bottom: Mean chlorophyll-*a* and phaeopigment concentrations in surface sediments and *P. moseleyi* guts in Jan 1996. Mean enrichment factors relative to surface sediments are indicated by numbers above bars. Samples sizes are given in parentheses.

($n = 2$) (C. Smith *et al.,* 1986; C. Smith, 1992). Each photograph covered an area of 0.3 m^2, and *Chiridota* sp. were clearly visible as they extended from burrows to feed (C. Smith, 1992). Because this holothurian maintains only one feeding opening at the terminus of its horizontal burrow (C. Smith, 1992), the number of active burrow openings visible in the first frame of each series was used to estimate *Chiridota* sp. density. Active openings were identified by visible extension of a chiridotid in the first, or in a closely subsequent, frame.

c. Flux consumption estimates

We used two approaches to estimate the processing rate of recently settled particles by *P. moseleyi, Chiridota* sp., and *B. bairdii* in SCB: a *thorium-flux model* that we developed, and an *end-member mixing model* similar to that of Lauerman *et al.* (1997). Our

thorium-flux model estimates the flux of $^{234}Th_{xs}$ activity through the guts of deposit feeders, using the following equation:

$$TF = \frac{a \cdot gw \cdot D}{gt}$$

where TF is the flux of $^{234}Th_{xs}$ activity through the animal population (dpm m^2 d^{-1}), a is the mean weight-specific $^{234}Th_{xs}$ activity of the gut contents (dpm g^{-1}), gw is the average dry weight of gut sediments for the species in question (g), D is the population density (m^{-2}), and gt is the gut throughput time (d). TF was compared to the flux of $^{234}Th_{xs}$ to the seafloor as measured by the sediment traps and as estimated from seafloor inventories of $^{234}Th_{xs}$ (Fornes *et al.,* in prep.). Assuming steady state, the seafloor flux equals the seafloor $^{234}Th_{xs}$ inventory (obtained by integrating sediment profiles of $^{234}Th_{xs}$) multiplied by λ, the radioactive decay constant for ^{234}Th (0.029 d^{-1}).

As a comparison to the thorium-flux model, we also estimated consumption of the "fresh" particulate flux for the same three species in SCB using an *end-member mixing model* (Lauerman *et al.,* 1997). We calculated the proportion, P, of freshly deposited material in the gut of an animal using the following equation (cf. Lauerman *et al.,* 1997):

$$P = \frac{(a - ss)}{(C_o - ss)}$$

where ss = mean $^{234}Th_{xs}$ activity of surface sediment (0–5 mm), and C_o = the mean $^{234}Th_{xs}$ activity (dpm g^{-1}) of particulate material at time of capture in the sediment trap, i.e., "fresh," or zero-age material. This model assumes that the animals are feeding either on zero-age material or bulk surface sediment, that $^{234}Th_{xs}$ is homogeneously distributed among particles caught in the sediment traps, and that $^{234}Th_{xs}$ is a conservative tracer relative to gut throughput times (≤24 hr, see below). Measured $^{234}Th_{xs}$ activity of the sediment-trap material was corrected to an average time-of-capture, or zero-age, activity (C_o) using the following equation:

$$F \cdot T \cdot C_{avg} = \int_0^T C_o \cdot F \cdot e^{-\lambda t}\, dt$$

where C_{avg} is the measured bulk $^{234}Th_{xs}$ activity of trap material, F is the mass flux (g d^{-1}) into the trap, T is trap deployment interval (in this case, 32.8 days), and t is time since trap deployment. C_o and F are assumed to be constant over the trap deployment. Solving the above equation:

$$C_o = \frac{\lambda \cdot T \cdot C_{avg}}{(1 - e^{-\lambda T})}.$$

Fresh particulate flux, A (dpm m^{-2} d^{-1}) through the population was then estimated using the following equation:

$$A = \frac{P \cdot gw \cdot D}{gt}.$$

Published throughput times for deep-sea holothurians range from 16–24 hours (Deming and Colwell, 1982; Sibuet, 1988). *In situ* tracer experiments in SCB with *P. moseleyi* indicate throughput times of ~12 h (Galley, Smith and DeMaster, in prep.). Thus, we used 12 hours as the throughput time for *P. moseleyi* and the much smaller *Chiridota* sp. (cf. Penry and Jumars, 1987). Deposit-feeding gastropods have been found to ingest 0.4 to 25 times their body weight in sediment daily (Lopez and Levinton, 1987). *Bathybembix bairdii* has an average gut-content weight of 49 ± 3.3% (± s.e.) of dry body weight (unpublished data). If this species ingests 0.4–25 times its body weight per day, this translates to gut passage times of 0.4–20 h. Since deep-sea gastropods are likely to have gut throughput times roughly comparable to their shallow-water counterparts (Penry and Jumars, 1987), we used 24 hours as a conservative estimate of throughput time for *B. bairdii*. Mean gut dry weights were obtained by dissecting formalin preserved specimens of each species, and drying the guts at ~60°C for >24 hr. Standard errors were propagated through all calculations as relative errors using the methods of Hodges and Lehmann (1970).

We also calculated the mass flux of sediment through *P. moseleyi, Chiridota* sp., and *B. bairdii* using a *mass-flux model*. Mass flux, M (g m^{-2} d^{-1}), through a megafaunal population was estimated as follows:

$$M = \frac{gw \cdot D}{gt}.$$

Apparent ^{234}Th ages of sediments relative to reference material (sediment-trap material or surface sediment) were calculated using the following equation:

$$t_a = \frac{\ln A_0 - \ln A_t}{\lambda}$$

where t_a is apparent age, A_0 is the $^{234}Th_{xs}$ activity of the reference material at time zero and A_t is the $^{234}Th_{xs}$ activity of the sample (=activity of the reference material at age t).

4. Results

a. ^{234}Thorium measurements

Surface-deposit feeders in Santa Catalina Basin had gut $^{234}Th_{xs}$ activities 23–261 times greater than that of average surface (0–5 mm) sediment (Table 1, Fig. 2). The epibenthic holothurians *P. moseleyi* and *S. globosa* had the highest gut $^{234}Th_{xs}$ activities, with corresponding apparent gut-sediment ages, relative to sediment-trap material, of −11 to 14 d (Table 1). The gastropod *B. bairdii* and the burrowing holothurian *Chiridota* sp. had lower gut $^{234}Th_{xs}$ activities, and apparent gut sediment ages of 28 to 98 d (Table 1). The molpadiid holothurian, a subsurface-deposit feeder, had an average gut $^{234}Th_{xs}$ activity lower than that of surface sediment at the time of collection (Dec), with an apparent gut-sediment age relative to surface sediment of 51 d (Table 1, Fig. 2). Nevertheless, the gut activity of the molpadiid was substantially higher (mean = 4.3 dpm g^{-1} vs 0 dpm g^{-1})

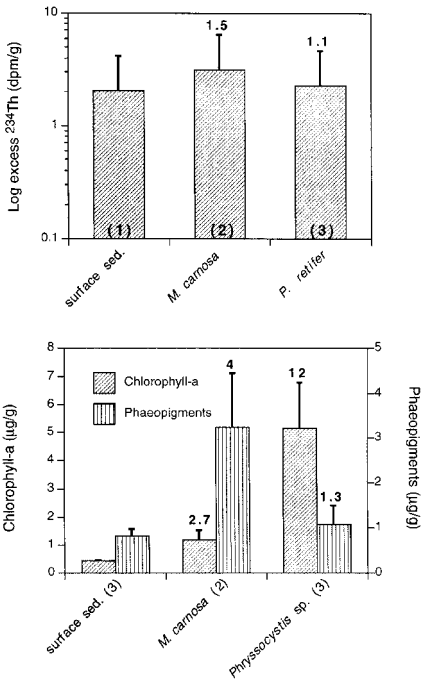

Figure 3. Mean $^{234}Th_{xs}$ activities (top), and chlorophyll-*a* and phaeopigment concentrations (bottom) of surface sediment (0–2 mm) and deposit-feeder guts on the Hawaiian slope. Note that $^{234}Th_{xs}$ activities are plotted on a log scale. Numbers in parentheses are sample sizes. Mean enrichment factors relative to surface sediments are indicated by numbers above bars. Error bars are one standard error with the exception of the $^{234}Th_{xs}$ for surface sediment ($n = 1$), which is a 1 σ counting error (see text).

than mean sediments at the 6–7 cm depths at which we presume these 6–7 cm long, head-down deposit feeders to be feeding (Table 1).

Gut sediments of two surface-deposit-feeding holothurians from the Hawaiian slope, *M. carnosa* and *P. retifer,* showed no significant enrichment of $^{234}Th_{xs}$ activity relative to surface sediment (Table 1, Fig. 3). It should be noted, however, that the surface sediment value is based on a single sample, and seafloor $^{234}Th_{xs}$ activities often are highly variable within a site.

The corrected flux of $^{234}Th_{xs}$ activity into the sediment trap in SCB for the period 12/5/95–1/7/96 was 731 ± 6 dpm m^{-2} d^{-1}, and the mass flux was 0.364 ± 0.02 g m^{-2} d^{-1}. Based on seafloor inventories (Fornes, 1999; Fornes *et al.,* in prep.), the flux of $^{234}Th_{xs}$ activity to the SCB floor in December, 1995 was 1830 ± 160 dpm m^{-2} d^{-1}, while in January, 1996, it was roughly 5-fold lower, i.e., 374 ± 38 dpm m^{-2} d^{-1}. Mean surface-sediment and species-specific gut activities of $^{234}Th_{xs}$ in SCB were also 2–6 fold higher in December than in January (Table 1).

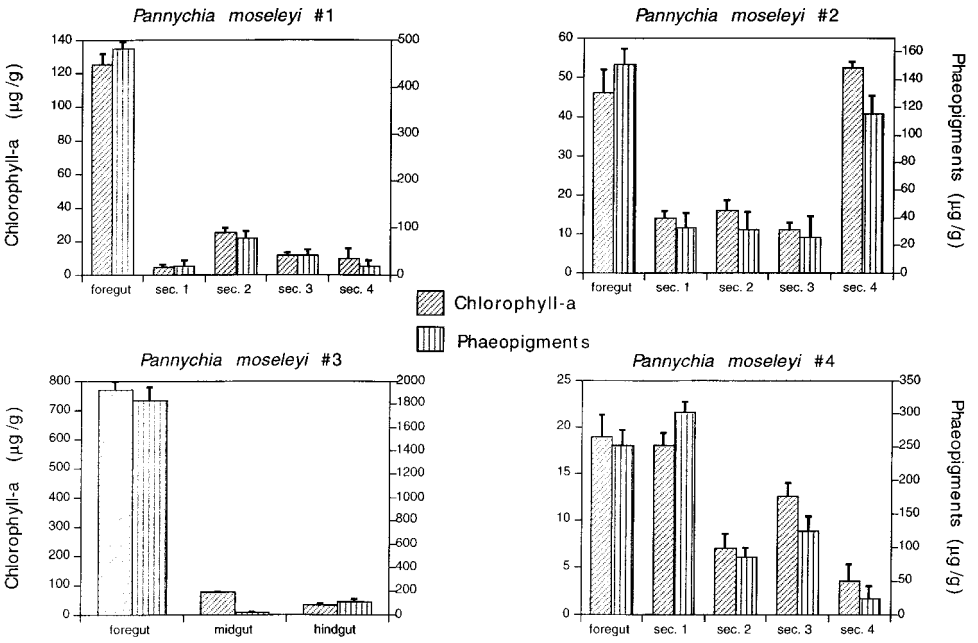

Figure 4. Mean chlorophyll-*a* and phaeopigment concentrations (±1 s.e.) along the guts of *Pannychia moseleyi* specimens from SCB, collected Mar 1996. Three measurements were made for each gut section.

b. Chlorophyll-a measurements

Concentrations of chl-*a* and phaeopigments were measured in the foreguts of one species in SCB, *P. moseleyi*. The average chl-*a* concentration was >500 times that of surface sediment (Table 1, Fig. 2). Chlorophyll-*a* was measured along the gut to provide indications of digestion and/or patchiness of food resources. Concentrations generally decreased along the *P. moseleyi* gut, with the foregut having the highest chl-*a* values in three of four cases (Fig. 4). On average, hindgut concentrations of chl-*a* were ~38% those in the foregut (Fig. 5). Phaeopigment concentration within the gut followed very similar trends.

On the Hawaiian slope, the foreguts of *M. carnosa* and *Phryssocystis* sp. had average chl-*a* concentrations 2.7 and 12 times greater than surface sediment, respectively (Fig. 3). Phaeopigments were also elevated 1.3–4 fold relative to surface sediments.

c. Population densities and mean gut weights

Based on time-lapse and survey photography, *Chiridota* sp. was by far the most abundant of the three prominent megafaunal surface-deposit feeders that we studied in SCB (Table 2). *Bathybembix bairdii* was approximately an order of magnitude less abundant than *Chiridota* sp., and *P. moseleyi* was roughly two orders of magnitude less abundant (Table 2). The mean individual weights of whole-gut sediments for these species

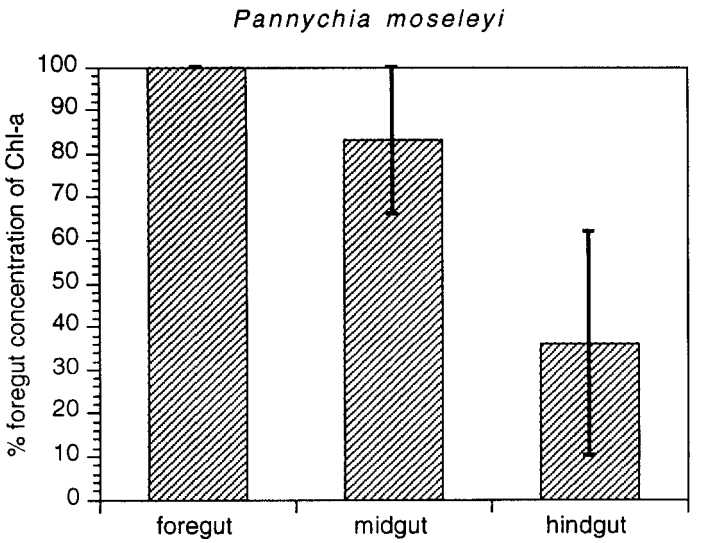

Figure 5. Mean (±1 s.e.) percentage of foregut chlorophyll-*a* concentrations in the fore-, mid- and hindguts of *Pannychia moseleyi* from SCB ($n = 4$). For individuals numbers 1, 2 and 4 (Fig. 4), gut sections 1 and 2 were combined for the midgut data, and sections 3 and 4 for the hindgut data.

were inversely related to population density, yielding roughly equivalent standing stocks of gut sediments within the three populations (Table 2).

d. Flux consumption estimates

Consumption rates of $^{234}Th_{xs}$ fresh particles, and sediment mass by *P. moseleyi, Chiridota* sp., and *B. bairdii* are summarized in Table 3. Based on the *thorium-flux model,* the three species combined consumed 380 ± 200 dpm d^{-1} of $^{234}Th_{xs}$ activity over Dec–Jan; this was about 50% of the daily sediment-trap flux of $^{234}Th_{xs}$ activity, and about 40% of the

Table 2. Mean individual gut weights, population densities, and standing stocks of gut sediments (±1 standard error) for the three dominant megafaunal surface-deposit feeders in Santa Catalina Basin.

Species	Gut dry weights (g)	Density (no./m^2)	Gut-sediment standing stock (g/m^2)
Pannychia moseleyi	1.94 ± 0.36 ($n = 12$)	0.026 ± 0.02	0.05 ± 0.04
Chiridota sp.	0.07 ± 0.02 ($n = 30$)	2.4 ± 0.6	0.17 ± 0.09
Bathybembix bairdii	0.3 ± 0.03 ($n = 10$)	0.164 ± 0.12	0.05 ± 0.04

Table 3. Summary of the fluxes of $^{234}Th_{xs}$, "fresh particles" and mass through the guts of animals (i.e., ingested), and the ratios of these gut fluxes to the respective sediment trap and seafloor fluxes. Means ± one standard error are given. The $^{234}Th_{xs}$ activity of sediment-trap material was 1960 ± 150, as corrected to average time zero activity (see text), and the flux was 731 ± 6 dpm/m^2/d. The $^{234}Th_{xs}$ flux calculated using seafloor inventories was 1830 ± 160 dpm/m^2/d (Dec.) and 374 ± 38 dpm/m^2/d (Jan.) (Fornes *et al.*, 1999). Particulate (mass) flux, measured via sediment traps, was 0.364 ± 0.02 g/m^2/day.

		Thorium-flux model			End-member mixing model			Mass-flux model	
Species	Date	$^{234}Th_{xs}$ ingested (dpm m^{-2} d^{-1})	% of trap $^{234}Th_{xs}$ flux ingested	% of seafloor $^{234}Th_{xs}$ flux ingested	% of fresh material in gut	Fresh particles ingested (g m^{-2} d^{-1})	% of fresh particle flux ingested	Mass ingested (g m^{-2} d^{-1})	% of trap mass flux ingested
Pannychia moseleyi	Dec. 1995	280 ± 180	38 ± 24	15 ± 9.8	100 ± 19	0.10 ± 0.08	27 ± 23		
Chiridota sp.		260 ± 100	36 ± 14	14 ± 5.8	38.2 ± 3.9	0.13 ± 0.07	36 ± 19		
Bathybembix bairdii		44 ± 30	6 ± 4	2.4 ± 1.7	44.2 ± 5.8	0.02 ± 0.02	6 ± 5		
T		**580 ± 300**	**80 ± 42**	**32 ± 17**		**0.25 ± 0.17**	**69 ± 47**		
Pannychia moseleyi	Jan. 1996	130 ± 83	18 ± 11	36 ± 23	65.7 ± 6.8	0.07 ± 0.05	18 ± 15		
Chiridota sp.		38 ± 15	5 ± 2	10 ± 4.1	5.6 ± 0.6	0.02 ± 0.01	5 ± 3		
Bathybembix bairdii		7.5 ± 5.0	1 ± 0.7	2.0 ± 1.4	7.1 ± 0.9	0.00 ± 0.00	1 ± 1		
T		**180 ± 100**	**24 ± 14**	**48 ± 28**		**0.09 ± 0.07**	**24 ± 18**		
Pannychia moseleyi	Dec. & Jan. mean	200 ± 73	27 ± 10	25 ± 10	82.9 ± 17.2	0.08 ± 0.07	23 ± 19	0.1 ± 0.0	27 ± 22
Chiridota sp.		150 ± 100	21 ± 14	12 ± 2.0	21.9 ± 16.3	0.07 ± 0.07	20 ± 19	0.3 ± 0.1	93 ± 50
Bathybembix bairdii		26 ± 18	4 ± 3	2.2 ± 0.2	25.7 ± 18.6	0.01 ± 0.01	4 ± 4	0.1 ± 0.0	14 ± 11
T		**380 ± 200**	**52 ± 27**	**39 ± 13**		**0.17 ± 0.15**	**47 ± 41**	**0.5 ± 0.3**	**135 ± 83**

seafloor $^{234}Th_{xs}$ flux, based on seafloor inventories (Table 3). *Pannychia moseleyi* ingested the largest fraction of this flux, (25–27%), followed by *Chiridota* sp. (12–21%, Table 3).

Based on the *end-member mixing model, P. moseleyi, Chiridota* sp., and *B. bairdii* together ingested an average of 47 ± 41% of the average "fresh" particle flux over the Dec–Jan sampling times (Table 3). Again, *P. moseleyi* ingested the largest proportion. The percentage of zero-age sediment (i.e., sediment-trap material) in the gut, based on this model, was highest in *Pannychia* (83%), and was substantially lower (22–26%) for *Chiridota* sp. and *B. bairdii* (Table 3).

The estimated flux of sediment mass through all three animal populations in SCB was 0.5 g m^{-2} d^{-1} (Table 3). Assuming a dry bulk sediment density of ~0.2 g ml^{-1} (Fornes *et al.* in prep.), these animals ingest a mass equivalent to the top 0.5 cm of SCB sediment in about 5 years.

5. Discussion

The gut contents of surface-deposit feeders in SCB were on average 24–176 times richer in $^{234}Th_{xs}$ than surface sediments (Fig. 2), suggesting that these animals were ingesting particles that had settled out of the water column within the last ~100 d. These results are in strong agreement with the age-dependent mixing hypothesis, which predicts that deep-sea deposit feeders feed preferentially on young, food-rich particles (C. Smith *et al.,* 1993).

Scotoplanes globosa and *P. moseleyi,* the elasipodid holothurians, had the highest weight-specific gut $^{234}Th_{xs}$ activities in SCB, indicating that they ingest very fresh and presumably food-rich sediments. The high gut $^{234}Th_{xs}$ activities no doubt result in part from feeding on a very thin veneer of surface sediment (i.e., ≪0.5 cm thick) with mucous-covered tentacles. However, because elasipodids are quite mobile (moving at rates of 0.3 to 3 m hr^{-1}; Lafond, 1967; A. Smith *et al.,* 1997), this selective feeding likely also results in part from rapid exploitation of horizontal patchiness in recently deposited, food-rich (and $^{234}Th_{xs}$-rich) particles (cf. Yager *et al.,* 1993). In fact, *S. globosa,* and other species of elasipodids, do aggregate on patches of algal detritus and in shallow depressions where particle deposition may be enhanced (e.g., Smith and Hamilton, 1983); in addition, *S. globosa* is at least occasionally attracted to baitfalls (Pawson, 1976; C. Smith, 1985). These observations, in combination with our $^{234}Th_{xs}$ and chl-*a* measurements, suggest that some elasipodids exploit meter-scale horizontal patchiness in "young," food-rich particles on time scales of hours to days.

While the gut $^{234}Th_{xs}$ activities of *Chiridota* sp. and *B. bairdii* suggest substantial selectivity for relatively young particles (i.e., with apparent ages of 28–98 days), these species appeared to be much less selective than the elasipodid holothurians in SCB. For *Chiridota* sp., this lower selectivity may result from reduced ability to exploit horizontal patchiness due to much lower mobility. *Chiridota* sp. in SCB has a maximum measured burrowing speed of 10.0 cm d^{-1} (mean = 6.5 cm d^{-1}) and while feeding extends a maximum of ~5 cm from its burrow (C. Smith 1992; G. Smith and C. R. Smith, unpublished data); thus, within a 24 hr period, a *Chiridota* individual can exploit patches no more

than 15 cm apart. In contrast, the gastropod *B. bairdii* can move at speeds comparable to elasipodids (up to 0.9 m hr^{-1}; Wheatcroft *et al.,* 1990) so its lower feeding selectivity is more likely to reflect differences in mechanisms of particle pickup and/or feeding strategies between snails and elasipodids (Lopez and Levinton, 1987; Penry and Jumars, 1987).

The 500-fold gut enrichment of chl-*a* in *P. moseleyi,* relative to surface sediments, reinforces the notion that freshly deposited phytodetritus may be an important food source for deep-sea animals (e.g., Billett *et al.,* 1988). Interestingly, the concentration of chl-*a* generally decreased along the gut of *P. moseleyi* (Fig. 5), suggesting that chl-*a* is degraded during gut passage. This contrasts with the result of Moore and Roberts (1994), who found little evidence of chl-*a* breakdown along the guts of three species of abyssal holothurians and suggested on this basis that phytoplankton material was not a direct source of nutrition to their holothurians.

On the Hawaiian slope, the surface-deposit feeding holothurians *M. carnosa* and *P. retifer* exhibited no enrichment over surface sediment (from a single core) in gut $^{234}Th_{xs}$ activities. However, the 2.7–12 fold enrichment of chl-*a* in the guts of *M. carnosa* and *Phrissocystis* sp. suggests that these animals are indeed selective deposit feeders. What then explains the low gut enrichments of $^{234}Th_{xs}$ in surface-deposit feeders on the Hawaiian slope relative to SCB? The answer most likely lies in differences in the depositional regimes between the two sites. SCB is a relatively quiescent basin, and our sampling site is located 14 km from the nearest slope. In contrast, the Hawaiian-slope site lies at the foot of a $\sim 22°$ slope more than 1000-m in height (Fig. 1). The Hawaiian site is thus likely to experience substantial downslope transport of resuspended sediments (Edsall, 1975; Garcia, 1996). Such transport will entrain older bottom sediment into the water column where it can scavenge ^{234}Th and effectively decouple $^{234}Th_{xs}$ activity from time of particle settling from surface waters. Stated differently, the average $^{234}Th_{xs}$-rich particle on the Hawaiian slope is not likely to be a food-rich, recent arrival from the euphotic zone, and $^{234}Th_{xs}$ activity thus would not be a good tracer of labile organic material. Enrichment of chl-*a* in the guts of the surface-deposit-feeders on the Hawaiian slope does suggest, however, that the deposit feeders feed selectively on phytodetritus newly deposited from the euphotic zone. Age-dependent mixing is, therefore, likely to occur on the Hawaiian slope, but we predict that $^{234}Th_{xs}$ activity profiles will not reflect it.

Lauerman *et al.* (1997) found high $^{234}Th_{xs}$ activities in the guts of two species of holothurians (*Abyssocucumis abyssorum* and *Oneirophanta mutabilis*) from 4100-m depths off central California, with the gut sediments of these holothurians exhibiting mean apparent ages (relative to sediment-trap material) of 12–13 days. Thus, as predicted by the age-dependent mixing hypothesis (C. Smith *et al.,* 1993), the selective ingestion of young, $^{234}Th_{xs}$-rich particles may be widespread among deposit feeders in quiescent deep-sea settings.

As expected, the guts of subsurface-deposit feeders were less enriched in $^{234}Th_{xs}$ than those of surface deposit feeders in SCB; *Molpadia* sp. had a mean gut $^{234}Th_{xs}$ activity at least 20-fold lower than any surface-deposit feeder (Fig. 2). The apparent age of sediments

in *Molpadia* sp. guts relative to surface sediment was ~50 days. Assuming that these holothurians are head-down conveyor-belt feeders like *Molpadia oolitica* (Rhoads and Young, 1971), they are subducting surface sediments to their feeding depth (~7 cm) within ~50 d, or they are feeding very selectively on $^{234}Th_{xs}$-rich subsurface sediment. It seems unlikely that the molpadiids are intermittently feeding directly on surface sediments, because, to our knowledge, neither surface feeding nor down-burrow hoeing (as in Levin *et al.,* 1997) has ever been observed in molpadiids. Most likely, the gut $^{234}Th_{xs}$ activities result from some combination of rapid conveyor-belt feeding and particle selection at depth, because at least some molpadiids appear to be selective feeders (Self *et al.,* in prep).

With the *thorium-flux model,* we estimated that the combined populations of *P. moseleyi, Chiridota* sp., and *B. bairdii* in SCB ingested an average of 52% (±27%) of the daily sediment-trap flux of $^{234}Th_{xs}$, and 39% (±13%) of the seafloor flux of $^{234}Th_{xs}$ based on sediment inventories (Table 3). The *end-member mixing model* yielded a very similar number, with 47% (±41%) of the daily flux of "fresh" particles into the sediment traps being consumed by these three species (Table 3). All three estimates have substantial uncertainties (Table 3). The major sources of error were (1) temporal variability in gut $^{234}Th_{xs}$ activities (December means were 2–7 fold greater than those in January (Table 1)), and (2) spatial variability in the population densities (Table 2). We have no reason to think that either of these error sources is biased. One potential source of bias to the flux-consumption estimates is the possibility of change in abundance of *Chiridota* sp. between 1987 (when time-lapse photographs were taken) and 1996. If *Chiridota* sp. were extremely rare in 1996, our estimates of the total flux consumed by the three megafaunal species would require revision downward by a factor of ~0.6 (i.e., roughly 30% of the daily sediment-trap flux of $^{234}Th_{xs}$ would still be consumed by SCB megafauna). However, the large numbers (thousands) of *Chiridota* sp. collected in each of our trawl samples (personal observations) suggests that these holothurians were still very abundant in 1995–1996. Based on the range in our two thorium-flux estimates (±one standard error), we conclude that *P. moseleyi, Chiridota* sp., and *B. bairdii* together consumed 39–52% of the daily $^{234}Th_{xs}$ flux to the SCB floor.

We assume that the flux of $^{234}Th_{xs}$ activity is a good proxy for labile POC reaching the SCB seafloor. Rapidly sinking, biogenic particles appear to carry most of the labile POC flux to the deep sea (e.g., Thiel *et al.,* 1989) and these particles also appear to be the main carriers of scavenged radionuclides such as ^{234}Th (Fowler and Knauer, 1986; C. Smith *et al.,* 1993). In quiescent deep-sea habitats where suitable measurements have been made, the fluxes of $^{234}Th_{xs}$ and POC are, as expected, very strongly correlated (e.g. Pope *et al.,* 1996; Lauerman *et al.,* 1997). Thus, ingestion of 39–52% of the daily $^{234}Th_{xs}$ flux implies that a similar percentage of the daily flux of POC is processed by *P. moseleyi, Chiridota* sp., and *B. bairdii* at the SCB floor.

Is it reasonable that 39–52% of the vertical flux of $^{234}Th_{xs}$ and POC to the SCB floor enters the guts of surface-deposit feeding megabenthos? Deep-sea holothurians (Khripounoff and Sibuet, 1980), and many shallow-water surface-deposit feeders (Lopez and

Levinton, 1987) exhibit assimilation efficiencies for bulk sedimentary POC on the order of 15%; this implies that *P. moseleyi, Chiridota* sp., and *B. bairdii* in aggregate may be assimilating and respiring roughly 6–8% of the vertical POC flux. Energetics studies of bathyal and abyssal benthic communities suggest that megafaunal deposit feeders, in aggregate, may easily respire this large a percentage of the seafloor POC flux (e.g., K. Smith, 1992). The injection rate of $^{234}Th_{xs}$ activity into the sediment column implied for *Chiridota* sp. also appears to be reasonable. Assuming that *Chiridota* sp. ingests 12% of the $^{234}Th_{xs}$ activity flux (Table 3) and defecates this activity into its burrow at a depth of ~1 cm (C. Smith, 1992), at steady state, at least 12% of the seafloor $^{234}Th_{xs}$ inventory should be buried below the 0–0.5-cm depth interval in SCB. The mean $^{234}Th_{xs}$ profile for SCB (Fornes, 1999) suggests that at least 12% of the seafloor inventory was indeed buried deeper than 0.5 cm. Thus, limited available data suggest that our calculated fluxes of POC and $^{234}Th_{xs}$ activity through megafaunal deposit feeders in SCB are reasonable.

Lauerman *et al.* (1997) used an end-member mixing model, based on ^{210}Pb in guts, surface sediments and sediment traps, to estimate that one holothurian species (*Abyssocucumis abyssorum*) processed 0.2–4% of the vertical particle flux to the abyssal seafloor off central California. Their estimate is substantially smaller than ours for at least two reasons. (1) *A. abyssorum* constituted only about 6% of the surface-deposit-feeding megafauna (holothurians and echinoids) at their site. (2) They used a gut throughput (or "residence" time) of 6 days for their holothurian, which is probably unreasonably long (Penry and Jumars, 1990; Billett, 1991). If a more reasonable gut throughput time of 24 hr is used, *A. abyssorum* is estimated to process 1.2–24% of the vertical particle flux, which is much more in line with our numbers for a holothurian with similar abundances, *P. moseleyi* (Table 3).

It should be noted that we base our particle consumption estimates in SCB on the flux of $^{234}Th_{xs}$ activity through deposit-feeder guts (the *thorium-flux model*) rather than on an *end-member mixing model* using ^{210}Pb (half-life = 22 y), as in Lauerman *et al.* (1997). $^{234}Th_{xs}$ is a more appropriate tracer for labile organic matter at the seafloor than ^{210}Pb because it decays on 100-day time scales similar to those of labile POC (e.g., Stephens *et al.,* 1997). In contrast, ^{210}Pb integrates processes occurring over time scales of roughly 100 yr. The *thorium-flux model* also is a better approach than the *end-member mixing model* for at least two additional reasons. (1) Its primary assumption is that $^{234}Th_{xs}$ is a good seafloor tracer for labile POC, while the *end-member mixing model* has a number of additional untested assumptions (in particular, that animals feed on either "zero-age" or bulk sediments, see Section d. *Flux consumption estimates*). Thus, the more direct *thorium-flux model* is likely to yield more accurate estimates of the ingestion rates of labile POC. (2) In quiescent habitats, gut fluxes based on the *thorium-flux model* can be compared to seafloor fluxes derived from sediment inventories of $^{234}Th_{xs}$. This allows one to estimate the percentage of vertical flux consumed without deploying sediment traps, making the approach logistically simpler and independent of sediment-trap biases.

The finding that megafaunal deposit feeders may ingest a large fraction of the vertical

POC flux in SCB has important geochemical and ecological implications. The organic material ingested by deposit feeders is chemically altered (Plante *et al.,* 1990), with some material assimilated for respiration and growth. Deep-sea holothurians, for example, have been shown to assimilate an average of 15% of the POC, 22% of the organic nitrogen, and 52% of the hydrolyzable amino acids from ingested deep-sea sediments (Khripounoff and Sibuet, 1980; Sibuet, 1988). The remainder is passed as feces, which are often still highly enriched in organic matter relative to surface sediment (e.g., Plante *et al.,* 1990). Deposit-feeder feces appear to foster enhanced rates of microbial decomposition and solubalization of organic substances (e.g. Deming and Colwell, 1982; Plante *et al.,* 1990), so the fecal deposits of surface-feeding megabenthos are likely to constitute major geochemical "hot spots" (cf. Aller, 1982). In addition to digestive alterations, *Chiridota* sp. appears to be an important bioturbator, subducting ~12% of the daily vertical POC flux to sediment depths of ~1 cm. The buried chiridotid fecal material is likely to be sequestered from the high microbial activity characteristic of the sediment-water interface (e.g., Webb and Montagna, 1993), promoting organic-matter preservation. Such subduction clearly may be regarded as age-dependent mixing, and may help to explain the high $^{234}Th_{xs}$ mixing rates measured in Santa Catalina Basin (C. Smith *et al.,* 1993).

The apparent control by megafauna of a large proportion of the food supply in SCB and off central California has profound implications for the entire benthic community. Subsurface-deposit-feeders and the relatively immobile sediment assemblage (bacteria through macrofauna) may have little access to roughly 50% of freshly deposited particles, with this material becoming available only after ingestion (and geochemical alteration) by the mobile megabenthos.

Fecal casts produced by mobile megafauna are likely to increase the patchiness of food resources, potentially promoting high species diversity in deep-sea sediments (Snelgrove *et al.,* 1992). If our results from SCB and those from central California (Lauerman *et al.,* 1997) are typical of the deep sea, then the mobile, surface-deposit-feeding megabenthos must substantially influence the structure, geochemistry and energetics of deep-sea ecosystems, and should be considered to be "keystone resource modifiers" (Levin *et al.,* 1997). The role of large mobile deposit feeders in modulating sediment geochemistry and energy flow clearly merits study in additional deep-sea habitats.

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